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Alberts, Bart B G T ; Selen, Luc P J ; Bertolini, G ; Straumann, D ; Medendorp, W P ; Tarnutzer, A A

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# **Dissociating Vestibular and Somatosensory Contributions to Spatial Orientation**

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## Abstract

Inferring object orientation in the surroundings heavily depends on our internal sense of direction of gravity. Previous research showed that this sense is based on the integration of multiple information sources, including visual, vestibular (otolithic) and somatosensory signals. The individual noise characteristics and contributions of these sensors can be studied using spatial orientation tasks, such as the subjective visual vertical (SVV) task. A recent study reported that patients with complete bilateral vestibular loss perform similar as healthy controls on these tasks, from which it was conjectured that the noise levels of both otoliths and body somatosensors are roll-tilt dependent. Here, we tested this hypothesis in ten healthy human subjects by roll-tilting the head relative to the body to dissociate tilt-angle dependencies of otolith and somatosensory noise. Using a psychometric approach, we measured the perceived orientation, and its variability, of a briefly flashed line relative to the gravitational vertical (SVV). Measurements were taken at multiple body-in-space orientations (-90 to 90deg, steps of 30deg) and head-on-body roll-tilts (30deg left-ear-down, aligned, 30deg right-ear-down). Results showed that verticality perception is processed in a head-in-space reference frame, with a systematic SVV error that increased with larger head-in-space orientations. Variability patterns indicated a larger contribution of the otolith organs around upright and a more substantial contribution of the body somatosensors at larger body-in-space roll-tilts. Simulations show that these findings are consistent with a statistical model that involves tilt-dependent noise levels of both otolith and somatosensory signals, confirming dynamic shifts in the weights of sensory inputs with tilt angle.

## **New and Noteworthy**

In this study, we combine different head-on-body tilt angles with psychophysics to adequately assess the different sensory contributions to the systematic SVV error and response variability. In addition, we compare behavioural data to Bayesian model simulations of multiple multisensory optimal integration models.

## **Introduction**

Inferring the orientation of objects in the surroundings heavily depends on our internal sense of direction of gravity. One way to test this internal sense is by using the subjective visual vertical (SVV) task. In this task, subjects are asked to align a visual line with the gravitational vertical while upright or roll-tilted. Previous studies have shown systematic errors in the response, which is typically small near upright, may shift away from head-in-space orientation for intermediate angles ( $< 60$  deg, called E-effect)(Müller, 1916), and can become quite substantial for larger roll tilts, biased toward the orientation of the head in space ( $> 60$  deg, called Aubert-effect or A-effect) (Aubert, 1861; Mittelstaedt, 1983; Mast and Jarchow, 1996; Jarchow and Mast, 1999; Van Beuzekom and Van Gisbergen, 2000; Van Beuzekom et al., 2001; Kaptein and Van Gisbergen, 2004; Vingerhoets et al., 2008; De Vrijer et al., 2008; Tarnutzer et al., 2009a, 2010; Clemens et al., 2011). It has also been shown that the trial-to-trial variability in the SVV responses increases with roll tilt (Schone, 1964; Schöne and Haes, 1968; Udo De Haes, 1970; Van Beuzekom et al., 2001; De Vrijer et al., 2008; Tarnutzer et al., 2009a, 2010; Clemens et al., 2011).

Although the SVV is commonly used in clinical routine to test for purely vestibular deficits (Brandt and Strupp, 2005), various studies have now shown that this estimate not only relies on vestibular signals, but also on proprioceptive signals, somatosensory signals and cognitive biases (Angelaki and Cullen, 2008; De Vrijer et al., 2008; Tarnutzer et al., 2009a, 2010; Clemens et al., 2011). Recently, Clemens et al. (2011) modeled the underlying computations based on Bayesian inference principles. The structure of their model, shown in figure 1, involves three stages: sensory input, coordinate transformation, and a signal combination stage.

[Figure 1 about here]

At the sensory stage, physical information about the orientations of the head-in-space, head-on-body and body-in-space is translated into sensory information by the otoliths, neck proprioceptors, and body somatosensors, respectively. Note that we refer to the sensory information by single inputs, although each of the three could be a collection of multiple sensory cues. For example, the body somatosensory cue may consist of signals from the cutaneous receptors that sense skin pressure and distortion, signals that relate to muscle tension, and/or interoceptive signals within the body (Mittelstaedt, 1995, 1996).

According to the Clemens et al. (2011) model, the head-in-space signal is not only measured directly by the otoliths, but it is also derived indirectly by combining head-on-body with body-in-space signals, which is performed at the coordinate transformation stage. Furthermore, through experience, the brain builds up an internal estimate about the head-in-space orientation, which is reflected by the prior in the model. To infer the Bayesian estimate of head-

in-space, all these signals are optimally combined by weighting them with their reliability (i.e. the inverse of their noise level). In the model, noise was assumed constant for the body and neck sensors and tilt-dependent for the otoliths (for more details, see the methods section). It has been shown that this model is able to explain the systematic error and variability of the SVV task in healthy subjects (Clemens et al., 2011).

However, the assumption of tilt independent body noise was recently challenged. Alberts et al (2015) tested patients with complete loss of bilateral peripheral-vestibular function. Despite absent vestibular sensory input, they observed a roll-angle dependent modulation of trial-to-trial SVV variability. To account for this finding, they suggested an extension to the model by Clemens et al. (2011): the noise term on the body somatosensors should be tilt-dependent rather than constant, similar to the assumption made for the otoliths (see figure 1).

Here, we tested whether tilt-dependent body somatosensors are a valid extension to the model. To this end we dissociate head-in-space and body-in-space orientations by manipulating head-on-body orientations. This manipulation capitalizes on the tilt-dependency of the noise in the head and body sensors, predicting different estimates of head-in-space when the body is roll-tilted. Note that the original Clemens et al. (2011) model did not include this provision because it was based on data collected with the reference frames of head and body sensors aligned, making it ambiguous as to whether the otoliths or body somatosensors should be modeled with tilt-dependent noise.

Two previous studies (Guerraz et al., 1998; Tarnutzer et al., 2010) already tested the SVV with dissociated head and body orientations, showing that head-based graviceptive signals provide the predominant input for internal estimates of the SVV. Neither of these studies, however, assessed the responses psychometrically, which is a requirement to put the model to the

test and determine how the individual sensory systems are weighted in the SVV. In the present study, we therefore measure the SVV psychometrically at multiple body-in-space orientations (90deg counter clockwise (CCW) to 90deg clockwise (CW) roll tilt in steps of 30deg) and multiple head-on-body orientations (30deg left-ear-down (LED) head-on-body tilt, aligned, and 30 deg right ear down (RED) head-on-body tilt, see top of figure 2), allowing for a dissociation of vestibular and somatosensory contributions to vertical perception. To test whether the tilt-dependent body somatosensors is a valid extension, we further compare subjects' performance with the predictions of the Bayesian optimal integration model including the tilt-dependent body somatosensory extension (figure 1B, more detail in methods section).

## **Materials and Methods**

### *Subjects*

Ten healthy human subjects participated in the study (7 male and 3 female, aged  $32 \pm 9$  years). Four subjects were familiar with the experimental protocol. All subjects provided written informed consent after receiving explanation of the experimental procedure. Experimental procedures were approved by the local ethics committee (cantonal ethics committee Zurich, KEK-ZH-2014-0428) and adhered to the 2013 Declaration of Helsinki for research involving human subjects. Subjects were free of any known neurological disorders and had normal or corrected-to-normal visual acuity. Normal peripheral vestibular function was confirmed by video-head-impulse testing of all six semicircular canals and ocular/cervical vestibular-evoked myogenic potentials.

## *Setup*

Subjects were tilted in the roll plane using a computer-controlled turntable with three motor-driven axes (prototype built by Acutronic, Bubikon, Switzerland). Participants were restrained to the seat using a four-point safety belt; a horizontal bar restrained movements of the legs. Subject-specific seat adjustments ensured that the center of rotation was aligned with subjects' intersection of the interaural and naso-occipital axis during whole-body roll tilt. The head was kept in the correct position using a thermoplastic mask tightly covering the head. In order to minimize changes in body configuration, vacuum cushions were positioned on both sides of the upper body and the upper legs, and one cushion between the legs. A luminous line (angular subtense 9.5 deg) with a bright dot at the end was projected onto the center of a sphere mounted 1.5 m in front of the subject. The center of rotation of the luminous line was aligned with the center of rotation of the turntable.

## *Experimental paradigm*

The SVV was tested at seven different body-in-space orientations, ranging from -90 deg to 90 deg at 30 deg intervals, in three head-on-body tilt conditions (-30 deg LED, aligned, or 30 deg RED, see figure 2). Each experimental run started with the onset of a fixation dot in the center of rotation of the luminous line. Next, the subject was rotated from upright to a randomly chosen roll angle at a constant acceleration and deceleration of the turntable of  $10 \text{ deg/s}^2$ . This value is a compromise between keeping repositioning time as short as possible and being comfortable for the subject. To overcome any lingering effect of semicircular canal stimulation on the SVV (Jaggi-Schwarz and Hess, 2003; Pavlou et al., 2003) and hence exclude postrotatory



torsional nystagmus influences (Tarnutzer et al., 2009b), we introduced a 10s waiting period after subjects reached a given roll angle. Subsequently, an auditory cue indicated the onset of a briefly flashed (30 ms) luminous line. Subjects used two buttons (left, L and right, R) to indicate whether the orientation of the luminous line was clockwise (CW) or counterclockwise (CCW) of the perceived vertical. Line orientations were selected randomly from a set of 11 line orientations, centered on a literature-based coarse estimate of the subjects' perceived vertical for that particular roll-angle (head-in-space systematic SVV error estimates from Clemens et al. (2011):  $0^\circ$  for upright and  $\pm 30^\circ$  head-in-space orientations,  $\pm 5^\circ$  in the direction of head tilt at  $\pm 60^\circ$ ,  $\pm 15^\circ$  in the direction of head tilt at  $\pm 90^\circ$  and  $\pm 30^\circ$  in the direction of head tilt at  $\pm 120^\circ$  head-in-space orientation). We used line orientation intervals of 3 deg, except when the body was upright (2 deg) since subjects are less variable when seated upright (Tarnutzer et al., 2010; Clemens et al., 2011). After all 11 line orientations were tested, the subject was rotated to a new pseudo-randomly drawn roll angle and the above procedure was repeated. The subject returned to the upright orientation when ten roll angles of the body had been addressed. Room lights were turned on, and head-on-body roll-tilt was checked with an angle meter (accuracy  $0.01^\circ$ ). Each roll angle was tested ten times, yielding 110 responses for the corresponding psychometric curve. In total, seven runs of ten roll angles accounted for one head-on-body condition with 7 different body-in-space orientations. Data of the three head-on-body conditions were collected in either three sessions of 45 minutes or two sessions of 90 minutes. The latter one took longer because a new thermoplastic mask had to be made within that particular session for a different head-on-body orientation.

One might argue that head-on-body tilt introduces a horizontal and vertical shift of the nasal-occipital axis from the center of rotation. We performed a control SVV experiment in

which two subjects were tested with the head and body aligned, and the nasal-occipital axis either aligned with the center of rotation or shifted  $\pm 4$ cm laterally. This value reflects the average maximum displacement of the nasal-occipital axis when the head is tilted relative to the body. Subjects were tested at 0 (maximum horizontal displacement) and  $\pm 90$  (maximum vertical displacement) degrees roll tilt. Results showed no significant influence of this shift on both the systematic SVV error (-4cm:  $t(5) = 0.56$ ,  $p = 0.60$ , +4cm:  $t(5) = 1.83$ ,  $p = 0.13$ ) and variability (-4cm:  $t(5) = -1.26$ ,  $p = 0.26$ , +4cm:  $t(5) = 1.91$ ,  $p = 0.11$ ).

#### *Data analysis*

For every combination of body-in-space and head-in-space orientation, performance was quantified by fitting a cumulative Gaussian function to the proportion of CW responses relative to line orientation (Wichmann and Hill, 2001):

$$P(x) = \lambda + (1 - 2\lambda) \frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^x e^{-(y-\mu)^2/2\sigma^2} dy$$

in which  $x$  represents the line orientation in space,  $\mu$  the perceived orientation of the gravitational vertical, and  $\lambda$  the lapse rate, accounting for stimulus-independent errors. The difference between the perceived,  $\mu$ , and actual gravitational vertical (which is  $0^\circ$ ) is the systematic (SVV) error. The width of the curve is determined by  $\sigma^2$ , which is inversely related to precision, and serves as a measure of the subjects' variability in the SVV task. Fits were performed using the MATLAB routine 'fminsearch'.

197

198 *Optimal integration model*

199 Figure 1A represents the theoretical framework to account for the observed behavior of  
200 subjects. Note that this framework is mainly based on previous work by Clemens et al. (2011),  
201 but contains an extension for the characteristics of somatosensory information. The model  
202 contains three stages of information processing: a sensory input, coordinate transformation and  
203 signal combination stage.

204 *Sensory input:* At this stage of information processing, physical information about the  
205 world is translated into sensory signals, denoted by a hat symbol (^). The otoliths sense the  
206 orientation of the head in space ( $\widehat{H}_S$ ), neck sensors measure the orientation of the head on body  
207 ( $\widehat{H}_B$ ), and body somatosensors respond to the orientation of the body in space ( $\widehat{B}_S$ ). It is assumed  
208 that all sensory signals are unbiased but corrupted with Gaussian noise with variance  $\sigma^2$ . This  
209 noise depends on several factors, including age, gender, height, which are all pooled into one  
210 sigma value per sensor. Previous studies suggested that the variance of the otoliths ( $\sigma_{HS}^2$ ) (Schöne  
211 and Haes, 1968; Tarnutzer et al., 2009a, 2010) and the body somatosensors ( $\sigma_{BS}^2$ ) (Alberts et al.,  
212 2015) is tilt-dependent. Based on these observations, we added tilt-dependent noise on the body  
213 somatosensors by allowing the variance in the sensory head-in-space and body-in-space signals  
214 to increase rectilinearly with tilt angle.

215

$$\sigma_{HS} = \alpha_{HS} * |H_s| + \beta_{HS}$$

$$\sigma_{BS} = \alpha_{BS} * |B_s| + \beta_{BS}$$

216

$\alpha$  reflects the proportional increase of noise with roll tilt and  $\beta$  represents the noise at zero degrees in space. The tilt-dependency of the otolith noise was already incorporated in the original model proposed by Clemens et al. (2011), but the tilt-dependent noise on the body somatosensors was not incorporated by this model since it was based on data collected with the head and body sensors aligned and hence could not distinguish it from tilt-dependent otolith noise.

*Coordinate transformation:* To infer an estimate of the orientation of the head in space, the brain can use the direct sensory information from the otoliths ( $\widehat{H}_{SD}$ ), or indirect sensory information by combining the body somatosensory ( $\widehat{B}_S$ ) and neck ( $\widehat{H}_B$ ) proprioceptive information. This indirect pathway involves a coordinate transformation:  $\widehat{H}_{SI} = \widehat{B}_S + \widehat{H}_B$ . Since the information from the individual sensors was represented by two Gaussian distributions centered on  $B_S$  and  $H_B$ , the indirect pathway is now a Gaussian distribution centered on  $(B_S + H_B)$  with variance  $(\sigma_{BS}^2 + \sigma_{HB}^2)$ .

*Signal combination:* At this stage, all available information is combined into a statistically optimal estimate of head orientation in space ( $\widehat{H}_S$ ). To account for the systematic SVV errors found at larger roll tilts ( $> 60^\circ$ ) we assume that the brain uses prior knowledge that the head is typically upright (MacNeilage et al., 2007; De Vrijer et al., 2008; Clemens et al., 2011). This prior knowledge is represented by a Gaussian distribution centered on  $0^\circ$  roll tilt with variance  $(\sigma_{HSP}^2)$ . According to the rules of Bayesian inference (Landy et al., 1995; Jacobs, 1999; Ernst and Banks, 2002; Bays and Wolpert, 2007; Clemens et al., 2011) it can be shown that:

239

$$\widehat{H}_S = w_{HD} * \widehat{H}_{SD} + w_{HI} * \widehat{H}_{SI} + w_{HP} * 0^\circ$$

240 with

$$w_{HD} = \frac{1/\sigma_{HS}^2}{(1/\sigma_{HS}^2 + 1/(\sigma_{HB}^2 + \sigma_{BS}^2) + 1/\sigma_{HSP}^2)}$$

$$w_{HI} = \frac{1/(\sigma_{HB}^2 + \sigma_{BS}^2)}{(1/\sigma_{HS}^2 + 1/(\sigma_{HB}^2 + \sigma_{BS}^2) + 1/\sigma_{HSP}^2)}$$

$$w_{HP} = \frac{1/\sigma_{HSP}^2}{(1/\sigma_{HS}^2 + 1/(\sigma_{HB}^2 + \sigma_{BS}^2) + 1/\sigma_{HSP}^2)}$$

241

242 In these equations,  $w_{HD}$ ,  $w_{HI}$  and  $w_{HP}$  are the weights (adding up to 1) of the direct,  
 243 indirect and prior information pathway. Following the rules of error propagation, we can show  
 244 that the variance of the integrated head-in-space estimate becomes:

245

$$\sigma^2(\widehat{H}_S) = w_{HD}^2 * \sigma_{HS}^2 + w_{HI}^2 * (\sigma_{HB}^2 + \sigma_{BS}^2)$$

246

247 in which the variance contributions of the direct and indirect pathways are represented by their  
 248 squared weights (Clemens et al., 2011).

249 Finally, to compute the orientation of the luminous line in space, the brain needs to  
 250 combine the head in space information with eye-in-head information ( $\widehat{E}_H$ ) and line-relative-to-

eye information ( $\widetilde{L}_E$ ). Whereas the latter is assumed to be unbiased, uncompensated ocular counterroll could cause a systematic SVV error in the eye-in-head information, resulting in E-effects in vertical perception. Previous work (Palla et al., 2006) showed that this can be represented as:

$$\widetilde{E}_H = -A_{OCR} * \sin(\widetilde{H}_S)$$

in which  $A_{OCR}$  denotes the uncompensated ocular counterroll. The systematic SVV error in line orientation ( $\mu$ ), hence the perceived gravitational vertical, is then calculated by the formula:

$$\mu(SVV) = (H_S - \widetilde{H}_S) + \widetilde{E}_H$$

The model thus assumes that the SVV task is performed in an eye-in-space reference frame. However, since both the eye-in-head information as well as the head-in-space information relies on a head-in-space signal, the model actually assumes a head-in-space reference frame for SVV processing.

### *Model simulation*

Figure 1B shows a forward simulation (bold lines) of the optimal integration model for the systematic SVV error and variability in the 30 deg LED (orange), aligned (cyan) and 30 deg RED (magenta) head-on-body roll-tilt conditions relative to the head-in-space orientation (left panel) and body-in-space orientation (right panel) of the subject. The simulations are based on

previously measured average values of the prior knowledge, head-on-body and ocular counterroll parameters of Clemens et al. (2011) ( $\sigma_{HB}^2$ ,  $\sigma_{HSP}^2$ ,  $A_{OCR}$ , first row of table 1) and body-in-space parameters from Alberts et al. (2015) ( $\alpha_{BS}$ ,  $\beta_{BS}$ ). The head-in-space parameter values ( $\alpha_{HS}$ ,  $\beta_{HS}$ ) are obtained by retrieving the optimal combination of tilt-dependent head-in-space parameters and tilt-dependent body-in-space parameters that account for a similar amount of variability in the aligned condition as the optimal combination of tilt-dependent head-in-space parameters and constant body-in-space parameters in the restricted model of Clemens et al. (2011) ( $\alpha_{HS}$ ,  $\beta_{HS}$  and  $\beta_{BS}$  in the second row of table 1). The shaded areas reflect the spread in model simulations, based on the variance in the free parameters. In addition to these two models that assume the integration of direct and indirect pathways, we also simulated a model with only the direct otoliths pathway, based on the noise values from Clemens et al. (2011) (third row of table 1).

**Table 1. Best-fit parameter values of previous studies used to simulate spatial orientation behavior in the full and restricted Bayesian optimal integration model**

Model	$\alpha_{HS}$ (°/°)	$\beta_{HS}$ (°)	$\alpha_{BS}$ (°/°)	$\beta_{BS}$ (°)	$\sigma_{HB}^2$ (°)	$\sigma_{HSP}^2$ (°)	$A_{OCR}$ (°)
<b>Full</b>	0.31±0.06	2.5±1.2	0.045±0.01	4.9±3.1	4.9±2.7	12.5±3.2	14.6±10.2
<b>Restricted</b>	0.16±0.06	2.4±1.2	x	10.8±3.1	4.9±2.7	12.5±3.2	14.6±10.2
<b>Reduced</b>	0.16±0.06	2.4±1.2	x	x	x	x	x

The dashed lines in the systematic SVV error and variability simulations of figure 1B represent the outcome of the optimal integration of the probability distributions in figure 1A. In this particular example, the subject was seated upright with the head tilted 30 deg RED on top of the body.

#### *Model evaluation*

Besides the full optimal integration model with a tilt-dependent noise term for the head-in-space (vestibular) and body-in-space (body somatosensors) signals, we also simulated the restricted Clemens et al. (2011) model with a constant noise term on the body somatosensors (parameters are in the second row of table 1). Furthermore, we also simulated a model with only the direct pathway (*reduced model*), hence without body and neck contributions, to test whether the assumption that the indirect pathway contributes to the SVV task. For evaluation of the three model versions we obtained negative log-likelihoods of each subject showing a goodness of fit of the model given the data. These were then tested with a likelihood ratio test, quantifying whether the likelihood of the Bayesian optimal integration model is significantly better explaining the data than the restricted or reduced model. We also report Bayes factors (BF) to quantify the increase in effect size of the full model relative to the restricted and reduced model (Wagenmakers, 2007).

## Results

### *Psychometric results*

Figure 2A shows the SVV performance of a representative subject for the three different head-on-body tilt conditions. For each head-on-body tilt condition, the probability of a clockwise (CW) response is plotted as a function of line orientation relative to the gravitational vertical for some exemplar combinations of head and body-in-space orientation (head-in-space orientations are denoted by H:, body-in-space orientations are denoted by B:). To obtain quantitative measures of the systematic SVV error and response variability (i.e. SD), we fit psychometric curves to the data in each condition. The systematic SVV error is captured by the line orientation



corresponding to 50% probability of a CW response (dashed horizontal lines); the response variability is captured by the width of the psychometric curve. Note that an increase in head-in-space orientation is accompanied by an increase in systematic SVV error (larger shift from 50% CW line orientation relative to 0°) in the direction of the orientation of the head. As shown, fitted curves are steeper when the head is upright (0°), suggesting that the subject is more precise around upright than when roll tilted.

[Figure 2 about here]

Figures 2B and 2C depict the systematic SVV error and response variability as a function of head-in-space orientation, respectively, based on the psychometric fits to all conditions. Filled data points represent the measures extracted from the psychometric curves in figure 2A. Results show that the unsigned error increases with larger head-in-space orientation, confirming the shifts seen at the psychometric level (figure 2A). Furthermore, systematic SVV error patterns show no differences for the three different head-on-body tilt conditions.

Response variability, however, demonstrates clear differences for the three different head-on-body conditions (Figure 2C). When the body and head are aligned (middle panel) the lowest variability is seen when both are aligned with the gravitational vertical. The subject is thus most precise in indicating the direction of vertical when seated upright. Variability increases at larger head-in-space orientations, but levels off from 30° to 90°, consistent with previous reports (De Vrijer et al., 2008; Clemens et al., 2011). However, when the head and body are,

dissociated (head-on-body,  $\pm 30^\circ$ ), variability peaks at  $60^\circ$  roll tilt in the direction of the head-on-body tilt, decreasing again with larger head-in-space orientations.

To distinguish between the contributions of the body and the head in spatial orientation, these data also need to be represented relative to body-in-space orientation. Figure 3 depicts the summary statistics (mean and standard error) across the ten subjects, plotted against both head-in-space orientation (left panels) and body-in-space orientation (right panels), generalizing the observations described in figure 2. The systematic SVV error of the three different head-on-body conditions overlaps when plotted against head-in-space orientation rather than body-in-space orientation, indicating that the SVV task is performed in a head-in-space reference frame. This overlap, however, cannot be seen in the variability plot. At small roll tilts ( $0^\circ$  and  $\pm 30^\circ$ ), the variability data of the three head-on-body tilt conditions seems to overlap when plotted against head-in-space orientation, whereas at larger roll tilts, the variability data show more overlap when plotted relative to body-in-space orientation.

[Figure 3 about here]

### *Model predictions*

The lines superimposed on the data in figure 3A represent model simulations of the full Bayesian optimal integration model specified in figure 1A. The shaded area surrounding these lines illustrates the standard error based on the noise of the various parameters (see table 1). The mean systematic SVV error across the 10 subjects is clearly captured by the model, whereas the

mean variability overlaps only at small roll tilts. At larger roll tilts the mean variability decreases again, whereas the model still predicts increasing variability.

### *Model evaluation*

To quantify the goodness of fit of the model given the data, we obtained negative log-likelihood estimates (-logl) by comparing the Bayesian optimal integration model estimates of systematic SVV error and variability to the responses of the subject (table 2). To test whether the models' assumption of an increase in body somatosensory noise with body tilt angle is warranted, we compared its performance with a restricted model, which contained a constant noise level on the body somatosensors. A likelihood ratio test of the two models (with one degree of freedom difference, which corrects for the additional parameter  $\alpha_{BS}$  in the full model relative to the restricted model ) resulted in the full model outperforming the restricted model in nine out of ten subjects (\*\*  $p < 0.05$ , \*  $p < 0.001$ ). We also tested whether inclusion of the indirect pathways in the model makes a significant contribution to the SVV. A likelihood ratio test of the full model versus this model (with three degrees of freedom difference) resulted in a significantly better account of the full model for all subjects ( $p < 0.001$ ).

**Table 2. Model evaluation by means of the negative log-likelihood and Bayes factors (BF)**

Subject	Direct + indirect pathway			Only direct pathway	
	-logl full model	-logl restricted model	BF full model vs restricted model	-logl reduced model	BF full model vs reduced model
S1	1051.4*	1070.7	>20		
S2	965.1**	967.4	0.2		
S3	732.6*	747.4	>20		
S4	881.3*	972.2	>20		
S5	814.2*	851.8	>20	> 6000	>20
S6	1333.8*	1419.5	>20		

<b>S7</b>	1102.7*	1154.5	>20	
<b>S8</b>	1253.2*	1277.3	>20	
<b>S9</b>	844.9*	855.8	>20	
<b>S10</b>	971.9	967.2	0	
<b>Mean±SD</b>	<b>995±193</b>	<b>1028±206</b>		

Furthermore, we calculated Bayes factors to quantify the increase in effect size between the proposed full model and the restricted and reduced model. Regarding the strength of evidence, Bayes factors larger than 20 indicate that the full model is decisive, whereas Bayes factors smaller than 5 indicate that the difference in models is not important (Jeffreys, 1998). Table 2 shows that eight out of ten subjects show a decisive increase in data explanation by the full model.

#### *Sensory weights*

Using the parameter estimates we can compute the variances of the individual sensors for each condition and roll-tilt angle. Based on these variances we can compute the individual weights of the various sensors. The larger the noise of a particular parameter, the smaller its weight will be. The distribution of the vestibular, body somatosensory and prior knowledge weights against head-in-space orientation is depicted in figure 3B for the different head-on-body roll-tilt conditions. Parameter values are taken from the full Bayesian optimal integration model (table 1). Results of the head and body aligned condition show that subjects rely mostly on vestibular information when they are seated around upright (the weight of the otoliths is near 1). This contribution declines as the head-in-space orientation increases, whereas sensory weights of the body somatosensory and prior beliefs increase. With head-on-body tilt, the weight of the body somatosensory information increases more strongly for orientations in the direction of head-on-body tilt, decreasing again for larger head-in-space orientations. Note the similarity

between the weight distribution of the body somatosensory noise and the variability patterns of figure 2, which is illustrative of the significant contribution of body somatosensors in vertical perception.

## Discussion

In this study, we examined the properties and contributions of vestibular and body somatosensory information in a subjective vertical (SVV) task. By comparing psychometric measures of the systematic SVV error and response variability at multiple roll tilt angles, with the head and the body aligned or dissociated by  $\pm 30^\circ$ , we found that both head-in-space and body-in-space orientation affect the SVV. A single response emerged for the three head-on-body conditions when the systematic SVV error was plotted as a function of head-in-space orientation. This curve, which shows that the systematic SVV error increases with larger head-in-space orientations, suggests that the SVV is processed in a (task-dependent) reference frame attached to the orientation of the head in space (figure 3A).

For all three head-on-body conditions, variability in the SVV was lowest when the head was upright in space, increasing for small roll tilts ( $< 60^\circ$ ), and decreasing again for larger roll tilts ( $> 60^\circ$ ). When the variability data was plotted against head-in-space orientation, the three head-on-body conditions overlapped for small roll tilts, but when plotted against body-in-space orientation it overlapped at larger roll tilts. These results indicate a larger contribution of the head sensors (otoliths) around upright and a more substantial contribution of the body somatosensors at larger roll tilts. Simulations showed that the data favored a model with tilt-dependent body somatosensory noise over constant noise (table 2), predicting the dynamic shift

from vestibular to somatosensory contribution to spatial orientation with increasing roll tilts (figure 3B).

#### *Comparison with previous (modeling) work*

The present findings on systematic SVV errors when the head and body are aligned are consistent with previous reports regarding spatial orientation (Aubert, 1861; Mittelstaedt, 1983; Mast and Jarchow, 1996; Jarchow and Mast, 1999; Van Beuzekom and Van Gisbergen, 2000; Van Beuzekom et al., 2001; Kaptein and Van Gisbergen, 2004; Vingerhoets et al., 2008; De Vrijer et al., 2008; Tarnutzer et al., 2009a; Clemens et al., 2011). Under the assumption that sensory signals are accurately calibrated (i.e. unbiased), this suggests, in a Bayesian framework, that prior knowledge about the head typically being upright drives the estimate of the visual vertical towards the orientation of the head in space (MacNeilage et al., 2007; De Vrijer et al., 2008; Tarnutzer et al., 2010; Clemens et al., 2011). Observations of the systematic SVV error when the head and body are dissociated confirm previous work by Guerraz et al. (1998) and Tarnutzer et al. (2010), who identified the head sensors (otoliths) as the major contributor to the systematic SVV error, suggesting that the SVV is processed in a head-in-space reference frame. In support of this notion, we show that model simulations of a statistical optimal integration model, which assumes that every piece of sensory information is transformed into a head-in-space coordinate system, overlap the data in all three conditions.

The novelty of our psychometric approach concerns an adequate assessment of the response variability. We show that response variability of individual subjects increases with roll tilts up to about 60° head-in-space orientation and decreases for larger head-in-space orientations

(figure 3A). It would be interesting, in future work with larger subject samples, to characterize the individual variation in this behavior to age and gender differences (Barnett-Cowan et al., 2010).

The increase in variability has been reported before (Schöne and Haes, 1968; Udo De Haes, 1970; Van Beuzekom et al., 2001; De Vrijer et al., 2008; Clemens et al., 2011) and attributed to an increase in vestibular noise with head-in-space orientation (Schöne and Haes, 1968; Tarnutzer et al., 2009a, 2010; Clemens et al., 2011), due to a non-uniform distribution of hair cells on the otoliths (Rosenhall, 1972, 1974; Fernandez and Goldberg, 1976; Tarnutzer et al., 2009a). This means that, when the head is roll-tilted in space, fewer hair cells code for that particular head-in-space orientation, leading to different firing rates (Tarnutzer et al., 2009a). In the architecture of the model this is captured as a tilt-dependency of the noise of the otoliths. The same suggestion has also been proposed for other sensory systems (Sober and Körding, 2012). Along these lines, recent clinical work from our group also suggested tilt-dependent body somatosensory noise for the estimation of the body-in-space orientation (Alberts et al., 2015). In this experiment it was shown that patients with complete bilateral vestibular loss had lower variability in a SVV task when seated upright than when roll-tilted 90°, which can only be attributed to extra-vestibular cues. Here, we confirm this suggestion by showing that a Bayesian optimal integration model including tilt-dependent noise on the body somatosensors predicts the response variability data significantly better than a model assuming constant somatosensory noise.

*Considerations for the model*

Simulations of the model presented in the current paper cannot fully capture the plateau and even decrease in response variability seen at larger roll-tilts of the head in space ( $> 60^\circ$ ). This observation, which has not been consistently reported before (but see Tarnutzer et al., 2009a), would have implications for previous modeling work (Eggert, 1998; MacNeilage et al., 2007; De Vrijer et al., 2008; Tarnutzer et al., 2009a; Clemens et al., 2011), as well as for the present model (figure 1). Which factors could be considered to account for the plateauing, or even reduction of response variability at larger head-in-space tilts?

We can rule out that there are artifacts in the control of the vestibular motion platform, i.e. all tilt angles are equally precisely controlled and adopted. We also consider further cognitive factors as less relevant. For example, while the current model assumes that the brain has built up an internal prior that the head is typically upright in space (as during daytime), the head and body are approximately roll-tilted  $90^\circ$  when lying on the side during night. Expanding the model's prior to include this notion, however, would introduce an additional SVV error, which we do not see in the data. Moreover, such a prior would also introduce systematic errors in the percept of subjective body tilt, which has not been reported either (Schöne and Haes, 1968; Mittelstaedt, 1983; Mast and Jarchow, 1996; Jarchow and Mast, 1999; Kaptein and Van Gisbergen, 2004; Clemens et al., 2011).

Perhaps a more tentative factor could relate to the contribution of extra-vestibular cues. In the present model we captured the tilt-dependency of the body somatosensors by a linear relationship, which may be an oversimplification. Somatosensory information consists of multiple cues, including those from the cutaneous receptors that sense the change in the distribution of pressure on the skin, from muscle tension that is increased, and/or from the putative visceral receptors in the trunk (Mittelstaedt, 1995, 1996). Early research has shown that



the thresholds to skin vibration decrease with increasing stimulus area (Verrillo, 1966; Makarov and Matoyan, 1968; Young, 1982). Since the projection of the body weight vector over a larger area of pressure (the side of the body) gradually increases for larger body-in-space orientations, one can speculate that the overall noise level could decrease with body-in-space orientation (figure 4, dot-dashed). If this signal is optimally integrated with other types of body sensors, whose noise levels increase with body-in-space orientation, overall body somatosensory sensory noise can become highly non-linear. In support of this notion, non-linear somatosensory noise patterns have been proposed for upward-downward accelerations (Nesti et al., 2014), as well as rotational velocities (Mallery et al., 2010).

To further understand the origin of the roll tilt dependent body noise, ideally the present experiment needs to be repeated in an environment in which a projection of the body weight vector, i.e. pressure on the body, is absent and the pure contribution of body somatosensory cues can be assessed. This could for example be done using water immersion and whole body casts (Anastasopoulos et al., 1999; Trousselard et al., 2003, 2004). On the other hand, it is also worth mentioning that subjects who actively adopt a laterally-tilted posture, while standing in a dark room, show similar SVV biases as in the vestibular chair in which body parts are padded and motion is induced passively (Van Beuzekom et al., 2001).

[Figure 4 about here]

*Model simulations model vs. fitting*

In the present study, we simulated the model based on parameters from existing literature. With the current set of parameters, the model including tilt-dependent body somatosensors better explains the data than a model with only roll-tilt dependent otoliths (see BF in table 2). We did not use the present data set to derive a new set of parameters for two reasons. First, figure 3B already shows that the contribution of somatosensory signals is highest at larger roll tilts. This automatically brings along the limitation that we cannot dissociate the two models at smaller tilt angles, since this would predict a pure vestibular contribution. Ideally, measurements should therefore be targeted at even larger roll tilt angles, up to 180°. However, at angles > 130°, (Kaptein and Van Gisbergen, (2004) have shown bimodal response behavior of the SVV, which would complicate the interpretation of such measurements. Therefore, the model was specifically intended to capture behaviour for angles up to 130. A second limitation is that the present study only dissociates the head from the trunk at  $\pm 30^\circ$ , whereas larger dissociations would be desirable for model fitting, but not comfortable for the subjects. A further solution to these limitations lies in testing the subjective body tilt task (SBT) with dissociated head and trunk contributions (Clemens et al., 2011).

In conclusion, we have tested the performance of ten healthy subjects in a psychometric SVV task with the head and body aligned or dissociated by 30° LED/RED head-on-body tilt. The resulting systematic errors and variability patterns reflect the different contributions of the various sensory signals. We verified that our theoretical framework including both tilt-dependent otolith and body somatosensory noise explains the data better than a framework with only tilt-dependent otolith noise. These findings establish a novel view on vertical perception and should be taken into account in future research.

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#### *Figure legends*

Figure 1. A) Schematic representation of the Bayesian optimal integration model. The model contains three different stages. In the sensory input stage, physical signals are translated to sensory signals ( $\hat{\cdot}$ ) which are assumed to be accurate, but contaminated with Gaussian noise. The Gaussian noise is assumed to be tilt-angle dependent for both the head-in-space ( $\widehat{H}_S$ ) signal from the otoliths and the body-in-space ( $\widehat{B}_S$ ) signal from the body somatosensors. In the coordinate transformation stage, the neck proprioceptive signal is used for a reference frame transformation of the body-in-space signal into an indirect head-in-space signal ( $\widehat{H}_{SI} = \widehat{B}_S + \widehat{H}_B$ ). In order to derive an optimal estimate of the head-in-space orientation ( $\widetilde{H}_S$ ), the cue combination stage of the model weights the indirect signal (green pathway) with the direct signal (blue pathway) and prior knowledge (red pathway) that our head is usually upright (centered around  $0^\circ$ ). The relative contributions of these pathways ( $w_{HI}$ ,  $w_{HD}$ ,  $w_{HP}$ ) depend on the Gaussian noise of the underlying signals. Finally, an optimal estimate of line-in-space is obtained for the SVV-task by combining  $\widetilde{H}_S$  with estimates of the eye-in-head orientation ( $\widetilde{E}_H$ ) and line-on-eye orientation ( $\widetilde{L}_E$ ). The latter

is assumed to be veridical. Note that the cue combination stage is essentially a multiplication of the underlying probability distributions, resulting in a posterior head tilt angle distribution. The individual probability distributions of the sensory signals and the head tilt posterior are based on the parameters in table 1 for the condition in which the body is upright and the head is tilted 30° RED. B) Simulations of the Bayesian optimal integration model for the systematic SVV error and variability (including standard errors, SE), plotted against head-in-space (left panels) and body-in-space orientations (right panels) in the three different head-on-body tilt conditions: 30° LED (orange), aligned (cyan) and 30° RED (magenta). Parameter values are based on previous research by Clemens et al. (2011) and Alberts et al. (2015). The dashed lines in the plots indicate the 30° RED condition shown by the probability distributions in A).

Figure 2. SVV adjustments in a representative subject for the different head-on-body tilt conditions. A) Proportion (P) of CW responses plotted against the line orientation relative to the gravitational vertical for different head-in-space (H) and body-in-space (B) combinations. Solid lines show the best-fit psychometric curves from which the SVV error (line-in-space orientation at which  $P(CW) = 0.5$ , dashed) and the variability (inversely related to the width of the curve) are extracted and plotted against head-in-space orientation in B-C. Systematic SVV error and variability measures from the psychometric curves in A) are plotted as filled symbols and completed with systematic errors and variability of the remaining combinations of head and body-in-space orientation (open symbols).

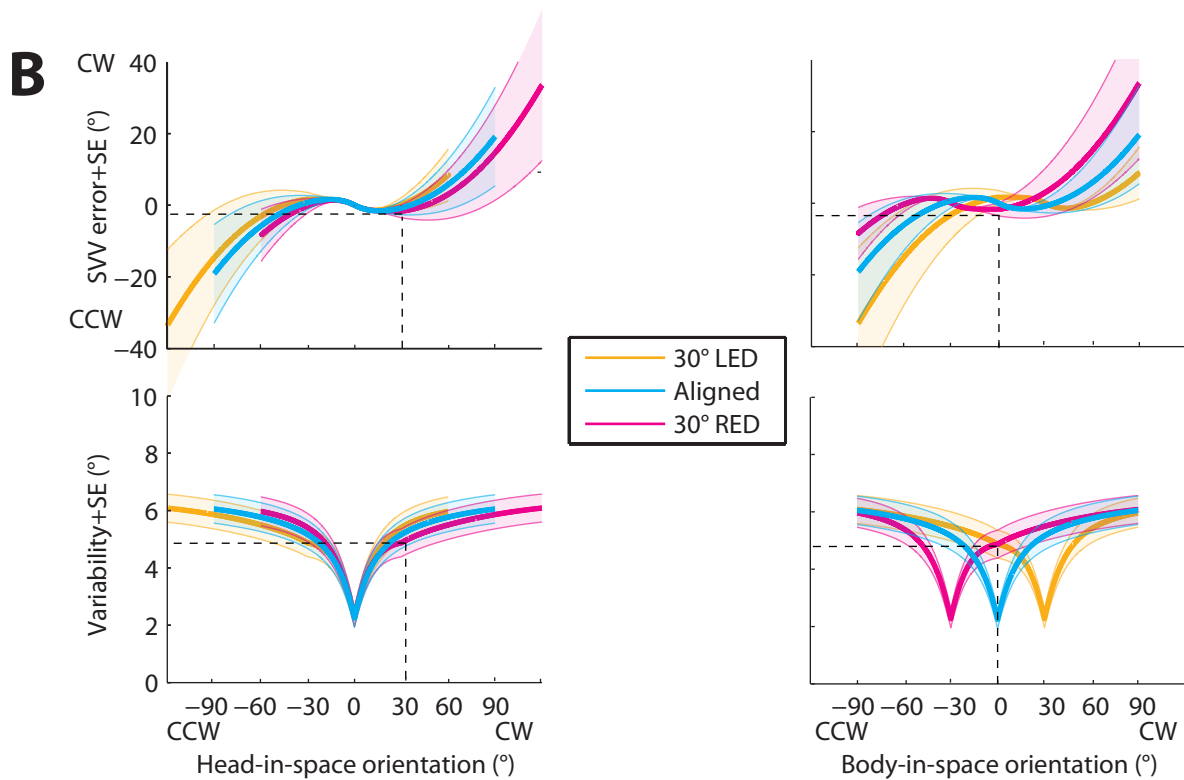
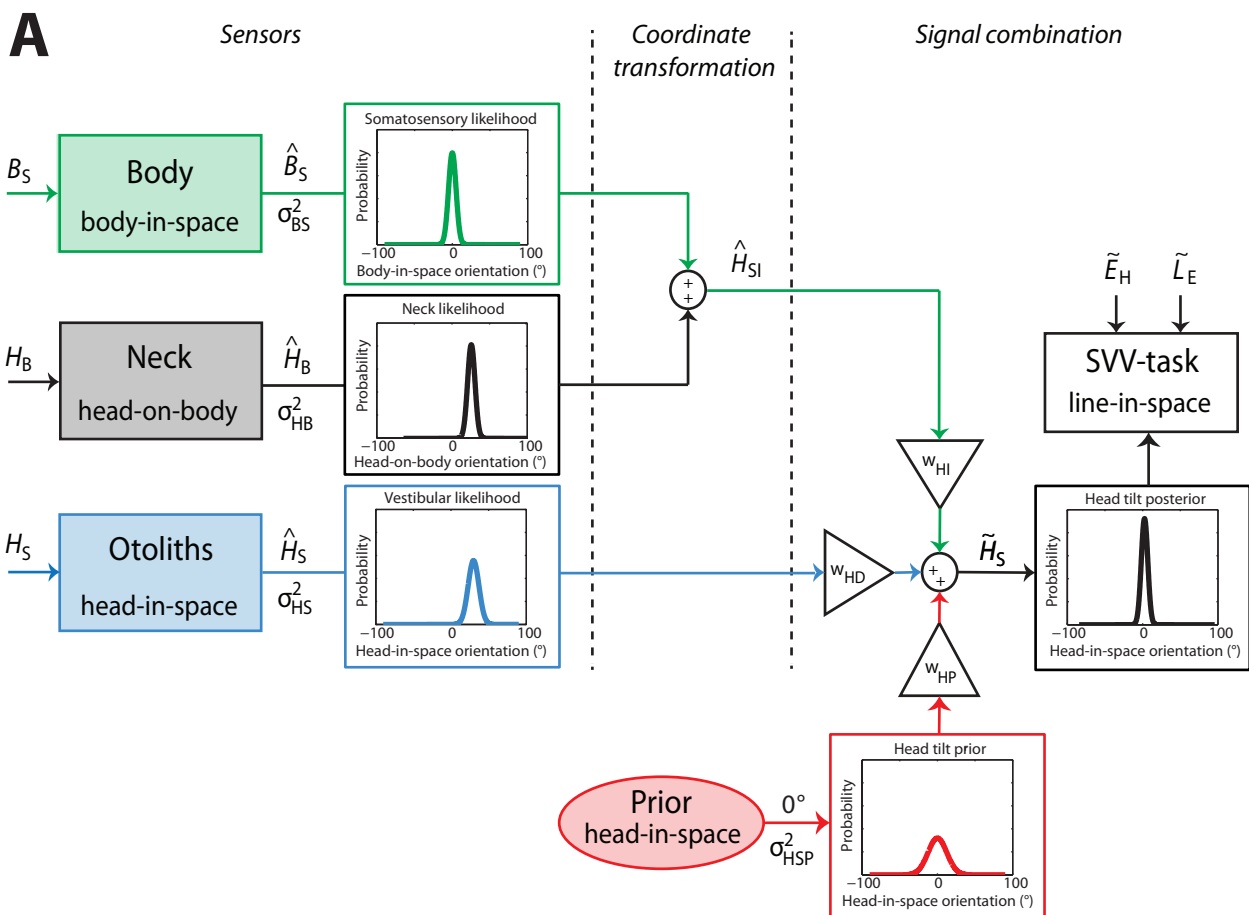
Figure 3. A) Mean systematic SVV error and variability (including one SE) across the 10 subjects are plotted against head-in-space orientation (left panels) and body-in-space orientation (right panels) for the three different head-on-body tilt conditions. Mean data is superimposed on the model simulations (including one SE) of figure 1B. B) Sensory weights of the different

664 sensors plotted against head-in-space orientation for the different head-on-body tilt conditions.  
665 Shaded areas are the variance in the sensory weights, based on the noise in the individual  
666 parameter settings of table 1.

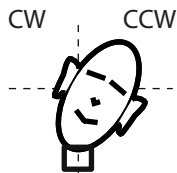
667 Figure 4. Simulations of the integration of trunk-graviceptive (solid) and cutaneous pressure  
668 sensors (dashed-dot) and the resulting body somatosensory dependent variability (dashed).  
669 Individual parameters are  $2.5^{\circ} + 0.05^{\circ}/^{\circ}$  tilt angle for the trunk graviceptive and  $3.5^{\circ} + 0.03^{\circ}/^{\circ}$   
670 tilt angle for the cutaneous pressure sensors. The latter is shifted  $90^{\circ}$ , such that the lowest  
671 variability occurs when subjects lie on the side.

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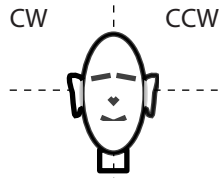




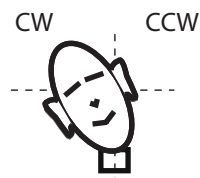
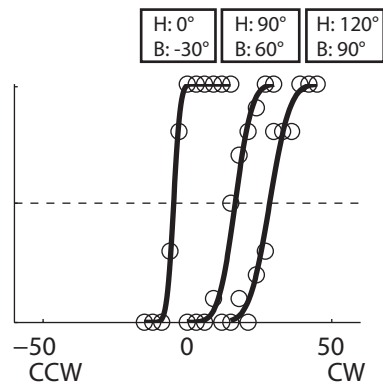
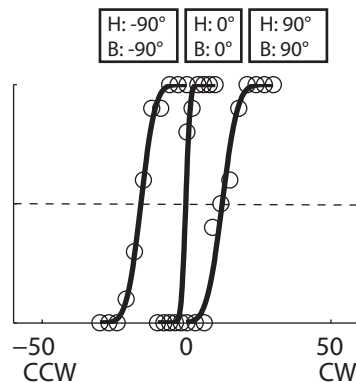
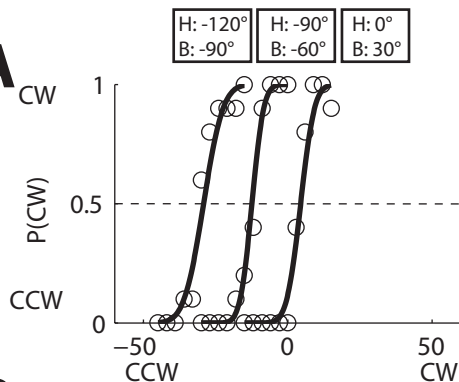
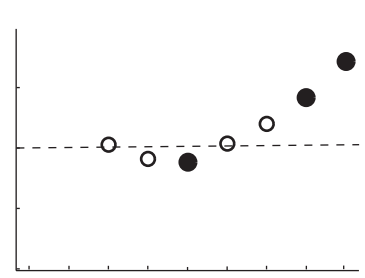
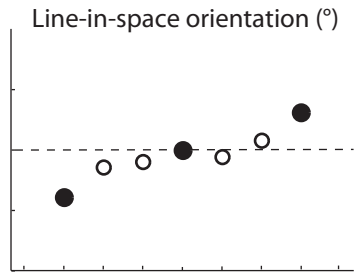
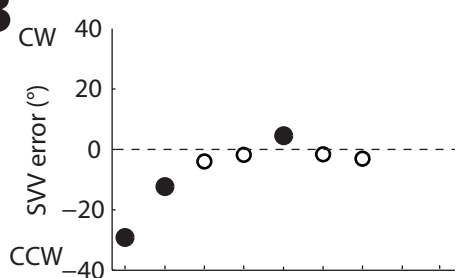
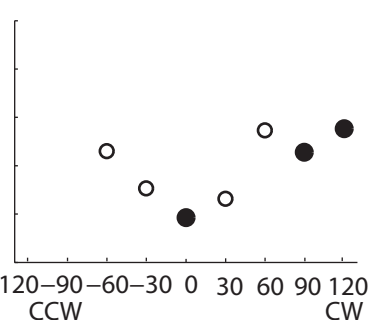
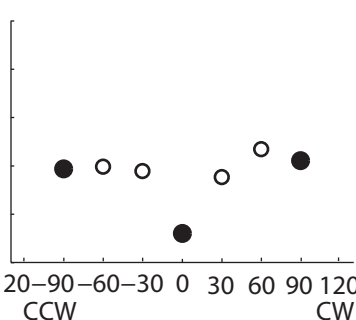
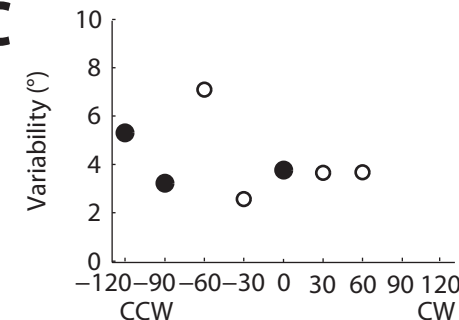
30° LED



Aligned



30° RED

**A****B****C**

Head-in-space orientation (°)

